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Food selectivity, feeding chronology, and energy transformations of juvenile Alewife (Alosa pseudoharengus) in the James River near Hopewell, Virginia

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FOOD SELECTIVITY, FEEDING CHRONOLOGY, AND ENERGY TRANSFORMATIONS OF JUVENILE ALEWIFE (<u>ALOSA</u> <u>PSEUDOHARENGUS</u>) IN THE JAMES RIVER NEAR HOPEWELL, VIRGINIA

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APPROVAL SHEET

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The chore of typing much of this manuscript and proofreading the rough and final copies befell Mary B. Tinsley. Her pleasant disposition never left her, as mine became progressively worse, and her invaluable aid is gratefully acknowledged.

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ABSTRACT

Juvenile alewife, Alosa pseudoharengus (Wilson), in the nursery area of the James River, Virginia usually exhibited a bimodal diurnal feeding periodicity. Mature calanoid and cyclopoid copepods, copepodite stages of copepods, and cladocerans were predominant prey during the day. Nocturnal feeding on ostracods, oligochates, and immature and mature insects was occasionally noted. In general, electivity (E) was strongly positive for the large adult copepods Eurytemora affinis, Cyclops vernalis, and the cladoceran Leptodora kindtii, moderately positive for the cladocerans Bosmina spp., neutral for copepodites, moderately negative for the cladoceran Diaphanosoma brachyurum, and strongly negative for copepod nauplii. The effects of selective predation on the zooplankton community were not as pronounced as those found in lake environments, although the relatively small Bosmina spp. increased in abundance during the period of maximum utilization of the nursery area by alosine fishes in both years.

Energy transformations by juvenile alewife in the nursery area of the James River were estimated in 1972 and 1973 by field and laboratory methods. Preliminary estimations of daily rations were determined directly by ash-free caloric value of stomach contents in alewife collected every three hours during 27-hour stations, with laboratory-derived corrections applied for caloric value remaining from prior meals at mean environmental temperature. Percent egested of the caloric content of ingesta was estimated in the laboratory. Mean wet weight of all fish collected each month was converted to dry weight and caloric equivalent based on caloric analysis of ten fish each month, and the differences in caloric value between time intervals were calculated for estimation of growth rates. The caloric value of the remainder, after growth was subtracted from assimilation, was assigned to maintenance, since laboratory estimates of respiration rates were consistently high possibly due to handling of the excitable fish.

Ash-free caloric value of fish biocontent, daily ration, egesta, assimilation, and respiration for an average fish increased from early summer through September in each year. Growth, as percent of assimilated energy, was 48% in 1972 and 37% in 1973 respectively. Mean maintenance efficiency was 52% in 1972 and 63% in 1973. Lower water temperatures in 1972 may partially account for these differences.

CHAPTER I

FOOD, FEEDING PERIODICITY, AND FEEDING ELECTIVITY OF JUVENILE ALEWIFE IN THE JAMES RIVER, VIRGINIA

ABSTRACT

Juvenile alewife in the nursery area of the James River during 1972 and 1973 usually exhibited a bimodal diurnal feeding periodicity. Mature calanoid and cyclopoid copepods, copepodite stages of copepods, and cladocerans were predominant prey during the day. Nocturnal feeding on ostracods, oligochaetes, and immature and adult insects was occasionally noted. In general, electivity (E) was strongly positive for the large adult copepods *Eurytemora affinis*, *Cyclops vernalis*, and *Mesocyclops edax* and the cladoceran *Leptodora kindtii*, moderately positive for the cladocerans *Bosmina* spp., neutral for copepodites, moderately negative for the cladoceran *Diaphanosoma brachyurum*, and strongly negative for copepod nauplii. The effects of selective predation on the zooplankton community were not as pronounced as those found in lake environments, although the relatively small *Bosmina* spp. increased in abundance during the period of maximum utilization of the nursery area by alosine fishes in both years.

INTRODUCTION

This report summarizes a two year investigation of feeding periodicity, food habits, and feeding selectivity in juvenile alewife, Alosa pseudoharengus (Wilson) in the nursery area of the James River, Virginia.

Anadromous alewife are found from Newfoundland (Winters, Moores, and Chaulk, 1973) to North Carolina (Bigelow and Schroeder, 1953). Spawning occurs in fresh or brackish water streams and accessible ponds (Belding, 1921), and migration to the parent stream may occur (Thunberg, 1971). Water temperature affects the timing of the spawning migration (Saila et al., 1972; Richkus, 1974). Ripe fish are taken in the James River from early February through mid May (Davis et al., 1970). Fertilized eggs adhere to any available substrate and 5 mm larvae emerge in two to six days depending on water temperature (Joseph and Davis, 1965). Transformation into the juvenile form takes place at about 28 mm (Mansueti and Hardy, 1967). Young alewife remain in fresh or brackish water through the summer and begin a seaward movement with falling autumn water temperatures. Sexual maturity occurs in three to four years and a given year class may contribute significantly to spawning runs for four to six seasons (Davis et al., 1970).

Feeding periodicity of juvenile alewife in the nursery grounds is unknown. Landlocked adult alewife feed principally during the day (Emery, 1973), and juveniles of closely related blueback herring (*Alosa aestivalis*) feed actively during the day with maximum stomach fullness at dusk (Burbidge, 1974). Feeding chronology studies on other fishes indicate a wide variety of feeding activities (Darnell and Meierotto, 1962; Keast and Welsh, 1968; Mathur, 1971; Mathur and Robbins, 1971; Mathur, 1973; Swenson and Smith, 1973; Baumann and Kitchell, 1974). Feeding periodicity investigations aid in understanding natural patterns of food intake and in formulating daily ration estimates (Chapter II).

Foods of juvenile alewife in a quantitative sense are unknown for the anadromous population. The principal food organisms are immature and mature copepods, cladocerans, and ostracods (Belding, 1921; Davis and Cheek, 1967; Davis et al., 1970). Selective feeding on large zooplankters and its effect upon the plankton community has been established for landlocked populations of alewife (Brooks and Dodson, 1965; Brooks, 1968; Norden, 1968; Hutchinson, 1971; Warshaw, 1972). Juvenile blueback herring in the James River selected for large adult copepods and against copepod nauplii; selection was moderate to weak for copepodites and *Bosmina* sp. (Burbidge, 1974). Various life stages of yellow perch (Galbraith, 1967; Siefert, 1972; Wong and Ward, 1972), walleye (Houde, 1967), gizzard shad (Cramer and Marzolf, 1970), bigmouth buffalo (Starostka and Applegate, 1970), rainbow trout (Galbraith, 1967), emerald shiner, rainbow smelt, and bluegill (Siefert, 1972) are known to exhibit differing degrees of size-selective behavior. Food and feeding electivity studies are used in descriptions of feeding behavior of fishes, inter- and intraspecific competition among fishes, and interspecific relationships between a predator and its prey. Recent constructive criticisms of Ivlev's (1961) index of electivity (O'Brien and Vinyard, 1974) are considered in this electivity analysis of juvenile alewife.

STUDY AREA

The James River drains a 26,000 km^2 basin in the 539 km from its origin in western Virginia to its mouth at Hampton Roads (Va. Div. Water Resources, 1969). Tidal fluctuations extend 176 km from Hampton Roads to the fall line at Richmond, and saltwater intrudes an average 65 km (Brehmer and Haltiwanger, 1966). Average freshwater flow as measured at Cartersville is 198 m^3/s. The maximum discharge on record was 10,300 m^3/s (June 23, 1972) during Tropical Storm Agnes (U.S. Dept. Interior, 1973).

The upper 89 km of the tidal portion of the James River is characterized by abundant phytoplankton, scarcity of benthos, high concentration of phosphorus and organic nitrogen, heavy particulate load, and low dissolved oxygen concentrations at times due to domestic and industrial effluents from Richmond and Hopewell (Brehmer and Haltiwanger, 1966; Brehmer, 1967). The river in the vicinity of Hopewell (115-125 km from the mouth) was chosen for study because zooplankton abundance is very high relative to the remainder of the nursery area (Burbidge, 1974), and young-of-the-year alosines are numerous (Davis et al., 1970).

MATERIALS AND METHODS

Feeding Periodicity - Food. A 12-minute surface tow and a midwater tow (approximately 5 m) for juvenile alewife were made with a 1.5 m x 1.5 m Cobb trawl (13 mm mesh with 4 mm cod end liner) from an 11 m vessel (*W.K. Brooks*) at a speed of about 3.8 knots. Tows were repeated every three hours during a consecutive 27-hour period beginning one hour before sunrise once each month from July through September 1972 and June through September 1973. Flooding due to Tropical Storm Agnes precluded the scheduled June 1972 sample. From June through August, five sample intervals each 27-hour period were within predominately daylight hours and four sample intervals were within night periods; the opposite sample allocation occurred during September in both years.

Up to 25 alewife from each surface or midwater tow were frozen on dry ice in sealed plastic bags for analysis of feeding periodicity. Up to 5 alewife from each tow were preserved in 10% buffered formalin for food habits, feeding periodicity, and feeding electivity analyses. Fish placed in formalin did not regurgitate stomach contents. In some cases an additional 12-minute surface or midwater tow was taken during a sample interval if an inadequate number of alewife was obtained in the standard tow regime.

Frozen alewife were thawed in a refrigerator, measured to the nearest 1.0 mm (fork length), and weighed to the nearest 0.1 g after removal of excess moisture. Stomach contents from each fish were removed under a dissecting microscope and weighed to the nearest 0.1 mg.

Preserved fish were treated similarly to frozen fish except stomach contents were pooled for each depth and sample time after individually weighing for feeding periodicity. By combining stomach content weights of preserved and frozen fish, feeding periodicity was determined by the change in mg food/g fish (a measure of stomach fullness) over a 27-hour period. The pooled contents from preserved fish were examined in a gridded petri dish (5,809 mm^2) under a dissecting microscope for description of food habits. All prey species within five randomly selected grids (912 mm^2) were identified and counted, and the total number of each species was then calculated for each sample time.

Zooplankton. Two 3-minute plankton tows were made at both surface and midwater with a Clark-Bumpus sampler, equipped with a #20 (0.080 mm) mesh net and flow meter, every three hours concurrently with the fish tows. Zooplankton were preserved in a solution of soap, congo red, and 5% formalin. Each sample was diluted to a standard volume (125 ml) with water, and three 1 ml subsamples were individually examined in a gridded petri dish. All zooplankters, except Rotifera, within five randomly selected grids were identified and enumerated under a dissecting microscope. The average number of each species per liter of water sampled was calculated for each sample and values for replicate depth samples were averaged.

Electivity. Feeding electivity (selectivity) of juvenile alewife was calculated each month by relating the percent of each species in both surface and midwater plankton samples during the day to the percent of each species in the stomachs of fish collected at both surface and midwater during the day by Ivlev's (1961) index of electivity:

$$E = \frac{r_i - p_i}{r_i + p_i}$$

where : E = electivity

r_i = percent of species i in the stomach

p_i = percent of species i in the plankton

Electivity values range from -1 (total selection against a species) to +1 (total selection for a species); a value near 0 implies no active selection.

RESULTS

Feeding Periodicity. Wet weights of stomach contents from 677 juvenile alewife in 1972 and 1261 fish in 1973 were used to define the feeding periodicity. In 1972, stomachs of fish collected at midwater generally contained more food at a given sample time than those at the surface. In 1973, no definite trend was apparent. So, overall feeding periodicity was defined by averaging wet weight food (mg)/ wet weight fish (g) for fish captured at both surface and midwater for each sample time (Figs. 1 and 2).

The range in food intake was usually more pronounced during periods of peak feeding, but average values showed a definite feeding trend. Feeding began near dawn and a minor feeding peak occurred during the early morning hours in July 1972 and July through September 1973. During the late morning hours feeding intensity was reduced. Active feeding began again in the early afternoon and continued to a major peak about three hours before sunset in all months except Spetember 1972 and 1973 when the maximum stomach fullness occurred near sunset. Feeding during the night was light and digestion was the prominent process. The moon, at quarter stage, was visible on only one sample night (July 1973), and no increase in nocturnal feeding by alewife was observed.

Although fish captured later in the season in both years had more food in the stomachs at peak feeding times on an absolute weight basis, the proportion of stomach weight to fish weight decreased each month for both years, except in September 1973. Stomach contents were greatest for both years during the minor morning and major evening peaks in July 1972, about three weeks after massive flooding by Tropical Storm Agnes.

Food. The stomach contents of 209 alewife in 1972 and 298 fish in 1973 collected at both surface and midwater were examined for food analysis (Tables 1 and 2). Mean total number of organisms per stomach and mean weight of stomach contents were greatest during the daylight hours. The high number of organisms in the stomachs of fish collected at night during September 1972 and 1973 was mostly a reflection of the 2100 EST night sample which contained a large portion of undigested organisms presumably from the prior daylight feeding period. No completely empty stomachs were found during the day, but were frequently encountered during the night. The average number of prey per stomach for day samples gives the best indication of importance for prey taxa, since active feeding by alewife occurred mainly during the day, except on mature insects. Copepod nauplii were never a major item in alewife stomachs, but copepodite stages were important. Adult calanoid copepods, mainly *Eurytemora affinis* and rarely *Diaptomus reighardi*, were a dominant food especially in 1972. Average number of calanoids in the stomachs decreased from July through September 1972 and increased from June through September

1973. Average number of cyclopoid copepods, mainly *Cyclops vernalis* and *Mesocyclops edax* and rarely *Eucyclops agilis*, generally increased in the stomachs each month in both years. The harpacticoid copepod, *Canthocamptus robertcokeri*, was found in stomachs only in August 1973.

Cladocerans, mainly *Bosmina* spp. (*B. longirostris* and *B. coregoni*), *Diaphanosoma brachyurum*, and *Leptodora kindtii*, and less commonly *Alonella acutirostris*, *Moina brachiata*, *Ilyocryptus spinifer*, *Camptocercus macrurus*, *Leydigia acanthocercoides*, and *L. quadrangularis*, were found in greater numbers in the stomachs as the season progressed. The ostracod, *Physocypria exquisita*, was found occasionally in stomachs during 1972 and was a common item in stomachs during 1973.

The oligochaete, *Pristina breviseta*, and immature insects, *Chaoborus* spp. and *Procladius* sp., were consumed irregularly and in relatively small numbers. Mature insects, mainly minute Hemiptera, Diptera, and Hymenoptera, were usually prominent in stomachs of fish captured nearest pre-dawn and post-dusk. Most of the weight in stomachs during the night was due to mature insects and weighable but mostly unidentifiable remains of other prey.

Zooplankton. During July and August 1972, total zooplankton standing crop over 27 hours at surface and midwater was relatively low (Fig. 3). This was possibly due to flood and general high water conditions preceeding the sample dates. Standing crop increased appreciably in September 1972 due mainly to increased abundance of Bosmina spp. There were no major changes in zooplankton standing crop from June through September 1973.

There was no direct correlation between peak feeding times shown by feeding periodicity of alewife and total plankton abundance. Zooplankton was generally more abundant at midwater during the day in both years. Standing crop in 1972 was usually highest at the surface at night, but no definite pattern was evident in 1973.

Nauplii, generally the predominant organisms in the zooplankton (Figs. 4 and 5), were always more abundant at the surface during the day and night in 1972. Standing crop in the day was highest at the surface in June and July 1973 and at midwater later in the season. Nauplii were usually more abundant at midwater during the night in 1973.

Standing crop of Bosmina spp. was relatively high each month, with peaks occurring in September of both years. Copepodites were usually less abundant than Bosmina. Numbers of Bosmina and copepodites were generally highest at midwater during the day and at the surface at night, although differences between depths at night were often small.

The copepods Eurytemora affinis, Cyclops vernalis, and Mesocyclops edax and the cladoceran Diaphanosoma brachyurum occurred regularly in moderate numbers. E. affinis and C. vernalis were usually more abundant at midwater during the day and at the surface at night. Abundance of M. edax and *D. brachyurum* was usually highest at midwater during both the day and night.

The seven organisms cited above accounted for a monthly average of no less than 96% of the plankton during the day. The copepods *Diaptomus reighardi*, *Eucyclops agilis*, and *Canthocamptus robertcokeri*, the cladocerans *Ilyocryptus spinifer*, *Daphnia ambigua*, *D. parvula*, *Moina brachiata*, *Alonella acutirostris*, *Camptocercus macrurus*, *Leydigia acanthocercoides*, *L. quadrangularis*, *Alona guttata*, *A. quadrangularis*, and *Leptodora kindtii*, the ostracod *Physocypria exquisita*, the oligochaete *Pristina brevisita*, immature and mature insects, and conchostracans were encountered in variable but usually low abundance in the plankton.

Electivity. Although nauplii were always abundant in the water during the day, alewife exhibited a strong negative selection (Fig. 6). Alewife had a moderately negative to weakly positive selection for copepodites. Electivity for copepodites was lowest in September of both years when *Bosmina* abundance was very high. Selection was strongly positive for adult *Eurytemora affinis* in both years. Electivity for *Cyclops vernalis* was weakly negative to moderately positive in 1972 and strongly positive from July through September 1973. Selection was generally strong for *Mesocyclops edax*.

Alewife fed heavily on *Bosmina* spp. when the organisms were very abundant, and selection was moderately positive in most months. Electivity for Diaphanosoma brachyurum was moderately to strongly negative except in August 1973. Alewife selection for Leptodora kindtii, which was never abundant in the plankton, was strongly positive.

The eight prey species cited above accounted for no less than 88% of the stomach contents during the day for each sample month.

DISCUSSION

Juvenile alewife in the nursery area are predominantly diurnal in their feeding behavior, suggesting vision as an important sense for feeding. Active feeding may reflect responses to a combination of stimuli, such as sunlight levels (total radiation intensity or angle of light incidence), hunger, or prey availability. Peak feeding periods did not usually correspond with daily maximum total zooplankton density, but opportunistic feeding on adult insects occurred near dawn and dusk. Alewife began feeding shortly before dawn and a minor feeding peak, mainly due to zooplankton ingestion, was often noted about two hours after sunrise. The major feeding period occurred in the late afternoon about three hours before sunset in the summer months and about one hour before sunset in September 1972 and 1973. Copepodites, calanoid and cyclopoid copepods, and cladocerans were the predominant prey of alewife during the day. During the night, undigested or partially digested remains of daytime meals were present in the stomachs, particularly in the earlier portions of the night. Occasional nocturnal meals of immature and adult insects, ostracods, and oligochaetes were noted. Bimodal diurnal feeding patterns are reported for other fishes, such as yellow perch (Keast and Welsh, 1968) and blackbanded darter (Mathur, 1973).

Burbidge (1974) reported continuous feeding through the day by juvenile blueback herring (Alosa aestivalis) based on stomach weights. Feeding commenced at dawn and terminated near sunset with maximum stomach fullness observed at dusk. Massmann (1963) and Levesque and Reed (1972) reported greatest stomach contents in juvenile American shad (A. sapidissima) during the early evening near dusk. Massmann (1963) reported decreasing stomach contents from midnight to midday, when most stomachs were empty. Since these fish cooccur with alewife in the nursery area of the James River and feed on similar prey, different temporal feeding activity could lessen interspecific competition, as proposed by Keast and Welsh (1968) for fishes in Lake Opinicon, Ontario.

Juvenile alewife of the anadromous James River population choose prey selectively, as do landlocked populations (Brooks and Dodson, 1965; Brooks, 1968; Hutchinson, 1971). O'Brien and Vinyard (1974) discussed several factors that may affect the presentation of electivity indices: in terms of distribution, vertical and horizontal abundance of prey may change temporally and the abundance and feeding location of the predator may also vary.

The present study considered zooplankton and alewife captured near the surface and at midwater in the mid-channel area (about 10 m depth). Electivity was computed from average percentages of surface and midwater zooplankton and alewife contents over the entire day, so vertical and temporal distributional effects would be averaged. Any horizontal effects, such as differences in prey or predator activities and composition in shoal waters, would be missed. Daily changes in feeding patterns can prompt littoral and limnetic migration of fishes (Baumann and Kitchell, 1974) and this could occur with alewife.

Since sunlight is rapidly attenuated by the turbid waters of the nursery area in the James River (Hoagman et al., 1973) and since alewife presumably select prey by vision, feeding must occur predominately in near surface waters. However, catches of alewife per unit effort are usually greater at midwater during the day (Hoagman et al., 1973). Alewife may prefer a mid-depth habitat and seek prey intermittently or extendedly in upper lighted waters during peak feeding periods. Thus, alewife stomach contents from both surface and midwater samples should be used in the determinations of electivity. The electivity index would be affected by averaging the density of midwater zooplankton, where alewife may not feed, with surface abundance. Nauplii tended to be more abundant at the surface during the day and all other organisms, for which electivity was calculated, were generally more abundant at midwater. This method of analysis, however, seems justifiable until the relative numerical interchange between surface and midwater zooplankters is ascertained.

Alewife selected strongly for adult calanoid and cyclopoid copepods *Eurytemora affinis*, *Cyclops vernalis*, and Mesocyclops edax and cladoceran Leptodora kindtii and against copepod nauplii and cladoceran Diaphanosoma brachyurum. Selection was rather neutral overall for copepodites and moderately positive for Bosmina spp.

Evidence, in addition to calculated electivity values, is strong that alewife select prey rather than indiscriminately feed. Both particulate detritus and filamentous algae were abundant in plankton samples, but were seldom observed in stomach contents. Non-selective filter feeding would have concentrated these items in proportion to their abundance in the water, as Starostka and Applegate (1970) observed for Anacystis in bigmouth buffalo.

The extreme rarity of copepod nauplii in the stomach contents of alewife relative to their density in the plankton might suggest that alewife were structually unable to feed on these abundant forms. Brooks (1968), however, found alewife to select nauplii last when offered a mixture of adult Diaptomus minutus, metanauplii, and nauplii. Burbidge (1974) reported strong negative selection for nauplii by blueback herring in the James River near Hopewell, although selection was positive during two months in a downstream area where interspecific competition among fishes was greater for larger organisms and concentration of preferred prey was less. Planktivorous fishes, such as alewife and blueback herring, that feed selectively may find a suitable density of preferred prey near Hopewell, which would preclude the necessity of selecting for nauplii.

Brooks and Dodson (1965) suggested size, spatial distribution, abundance, palatibility, locomotory habits, and escape ability as factors affecting the availability of prey to a selective predator. The generally negative selection by alewife for the relatively large _Diaphanosoma brachyurum_ may be due to the rapid escape ability of the prey plus its habit of drifting motionless in the water (Brooks and Dodson, 1965). The moderately positive selection of _Bosmina_ spp. by juvenile alewife may reflect their high density and thus availability in the plankton. Hutchinson (1971) reported alewife to select positively for _Bosmina longirostris_ but the mean length of the prey in the stomachs was usually significantly greater than their average length in the plankton.

Selection by alewife or other planktivores for larger prey may result in qualitative and quantitative changes in the zooplankton community. In lake environments, as the larger planktonic species decrease in abundance under intensive predation, smaller species increase in density (Brooks and Dodson, 1965; Galbraith, 1967; Brooks, 1968; Wells, 1970; Hutchinson, 1971; Warshaw, 1972). Although it is presumable more efficient energetically for a predator to choose a few large prey rather than many small prey, there is a point, as smaller species become more abundant, where it is less costly to feed on any size found; this alternative spreads the mortality more equally among age classes of the smaller prey and promotes their survival

(Sprules, 1972).

Changes in zooplankton species composition, possibly due to selective predation, were not as pronounced in the James River as those reported for lentic environments. Larger organisms were present throughout the study period, although small *Bosmina* spp. increased notably in abundance from early summer through September in both years. The density of larger zooplankters in the nursery area may be partially maintained by the contribution of vertical distribution (i.e., larger forms were often more abundant at depths where light penetration is lessened or nil) and input from smaller tributaries, oxbows, or shoal areas where predation could be less extreme. In addition, intense predation by alosine fishes only occurs in the late spring, summer, and early fall after which the juveniles move seaward. Zooplankton populations may recover before the next pulse of active predation, and larger zooplankton species are not totally excluded, as occurs in lake environments, by the influence of size-selective predation.

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Table 1. Average number of organisms in stomachs of juvenile alewife collected at both surface and midwater during 1972 in the James River, Virginia.

	July 1972		August 1972		September 1972	
Organism	Day	Night	Day	Night	Day	Night
Nauplii	0.1	0.3	3.4	0.0	1.7	0.0
Copepodites	36.9	2.4	63.9	2.1	49.3	28.8
Calanoida	291.4	29.8	213.2	17.6	100.4	40.1
Cyclopoida	8.5	3.4	13.3	0.2	61.0	48.8
Harpacticoida	0.0	0.0	0.0	0.0	0.0	0.0
Cladocera	12.2	14.0	111.3	9.7	1773.8	1227.6
Ostracoda	0.3	0.0	2.1	0.0	0.0	0.0
Polychaeta	0.1	0.3	0.0	0.4	0.0	0.0
Immature Insect	0.0	0.0	0.2	0.8	0.7	0.0
Mature Insect	0.1	2.8	0.0	2.3	0.0	1.3
TOTAL	349.6	53.0	407.4	33.1	1986.9	1346.6

Table 1. (Continued)

Organism	July 1972		August 1972		September 1972	
	Day	Night	Day	Night	Day	Night
# Fish	50	21	30	34	26	48
$\bar{X}$ Length (mm)	48.3	50.0	55.9	57.9	73.1	77.4
$\bar{X}$ Weight (g)	1.5	1.7	2.4	2.7	5.2	6.4
$\bar{X}$ Stom. Wt. (mg)	20.0	8.1	19.2	3.9	34.6	23.9
# Empty	0	4	0	14	0	5

Table 2. Average number of organisms in stomachs of juvenile alewife collected at both surface and midwater during 1973 in the James River, Virginia.

Organism	June 1973		July 1973		August 1973		September 1973	
	Day	Night	Day	Night	Day	Night	Day	Night
Nauplii	0.7	0.0	0.2	0.0	0.0	0.0	1.3	0.0
Copepodites	3.0	0.0	21.4	0.2	29.5	3.5	25.2	5.5
Calanoida	8.7	0.2	18.2	1.4	28.1	0.7	29.7	6.0
Cyclopoida	0.3	0.3	25.8	0.4	40.6	0.6	27.1	5.0
Harpacticoida	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0
Cladocera	44.3	0.2	160.3	22.7	133.0	17.7	832.6	195.8
Ostracoda	0.0	0.0	2.7	1.9	9.8	5.6	0.0	5.5
Polychaeta	0.0	0.0	0.3	0.0	0.2	0.0	0.6	0.3
Immature Insect	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.5
Mature Insect	0.2	2.3	0.0	7.3	0.0	4.4	0.8	5.1
TOTAL	57.2	3.0	229.1	34.1	247.1	32.5	917.3	223.7

Table 2. (Continued)

Organism	June 1973		July 1973		August 1973		September 1973	
	Day	Night	Day	Night	Day	Night	Day	Night
# Fish	38	40	42	36	37	35	20	50
$\overline{X}$ Length (mm)	45.9	45.6	57.4	56.4	59.4	59.3	65.6	65.1
$\overline{X}$ Weight (g)	1.4	1.4	2.9	2.8	3.4	3.2	4.5	4.3
$\overline{X}$ Stom. Wt. (mg)	4.2	3.5	10.7	6.4	11.3	4.9	31.7	14.0
# Empty	0	6	0	5	0	4	0	1

Figure 1. Mean and range of food (mg wet weight food/ g wet weight fish) in juvenile alewife collected at both surface and midwater at three hour intervals in monthly 27-hour stations during 1972 in the James River, Virginia. [Number of stomachs examined indicated above each bar; horizontal light bars below times indicate daylight after sunrise (SR) and dark bars show darkness after sunset (SS)]

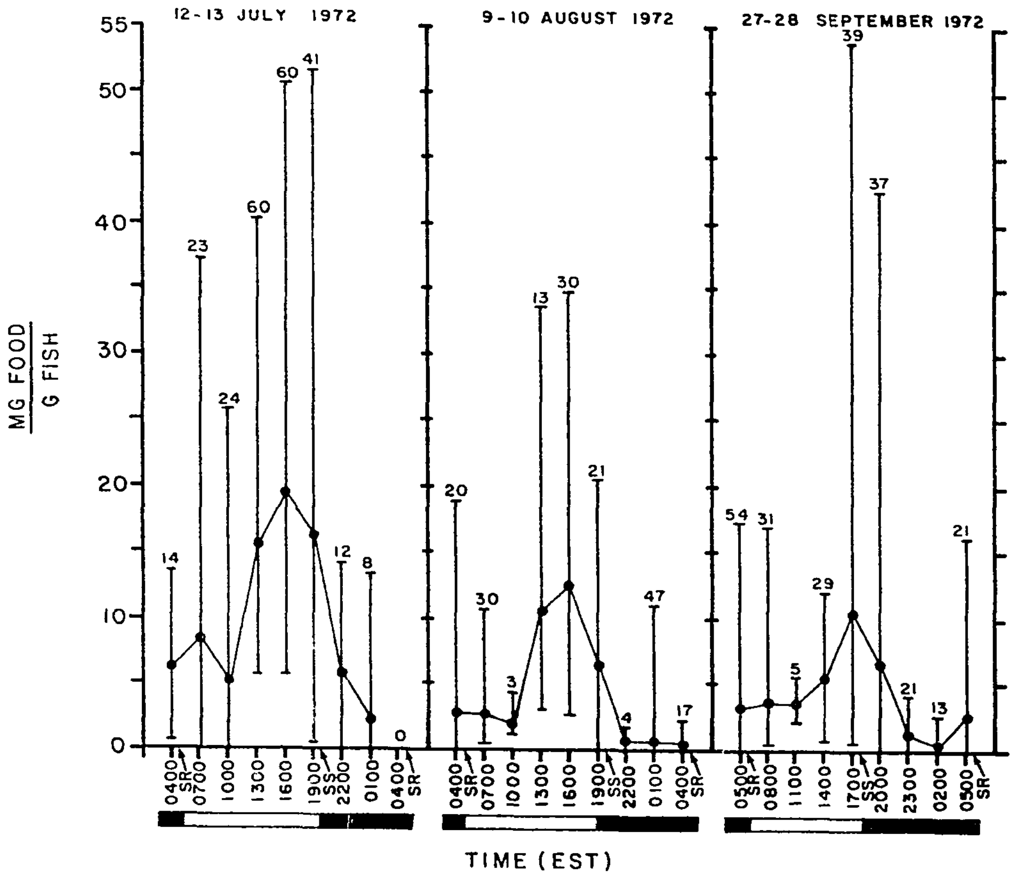

12-13 JULY 1972
9-10 AUGUST 1972
27-28 SEPTEMBER 1972
MG FOOD / G FISH
55
50
40
30
20
10
0
14
23
24
60
60
41
12
8
0
20
30
3
13
30
21
4
47
17
54
31
5
29
39
37
21
13
21
0400
SR
0700
1000
1300
1600
1900
SS
2200
0100
0400
SR
0400
SR
0700
1000
1300
1600
1900
SS
2200
0100
0400
SR
0500
SR
0800
1100
1400
1700
SS
2000
2300
0200
0500
SR
TIME (EST)

Figure 2. Mean and range of food (mg wet weight food/ g wet weight fish) in juvenile alewife collected at both surface and midwater at three hour intervals in monthly 27-hour stations during 1973 in the James River, Virginia. [Number of stomachs examined indicated above each bar; horizontal light bars below times indicate daylight after sunrise (SR) and dark bars show darkness after sunset (SS)]

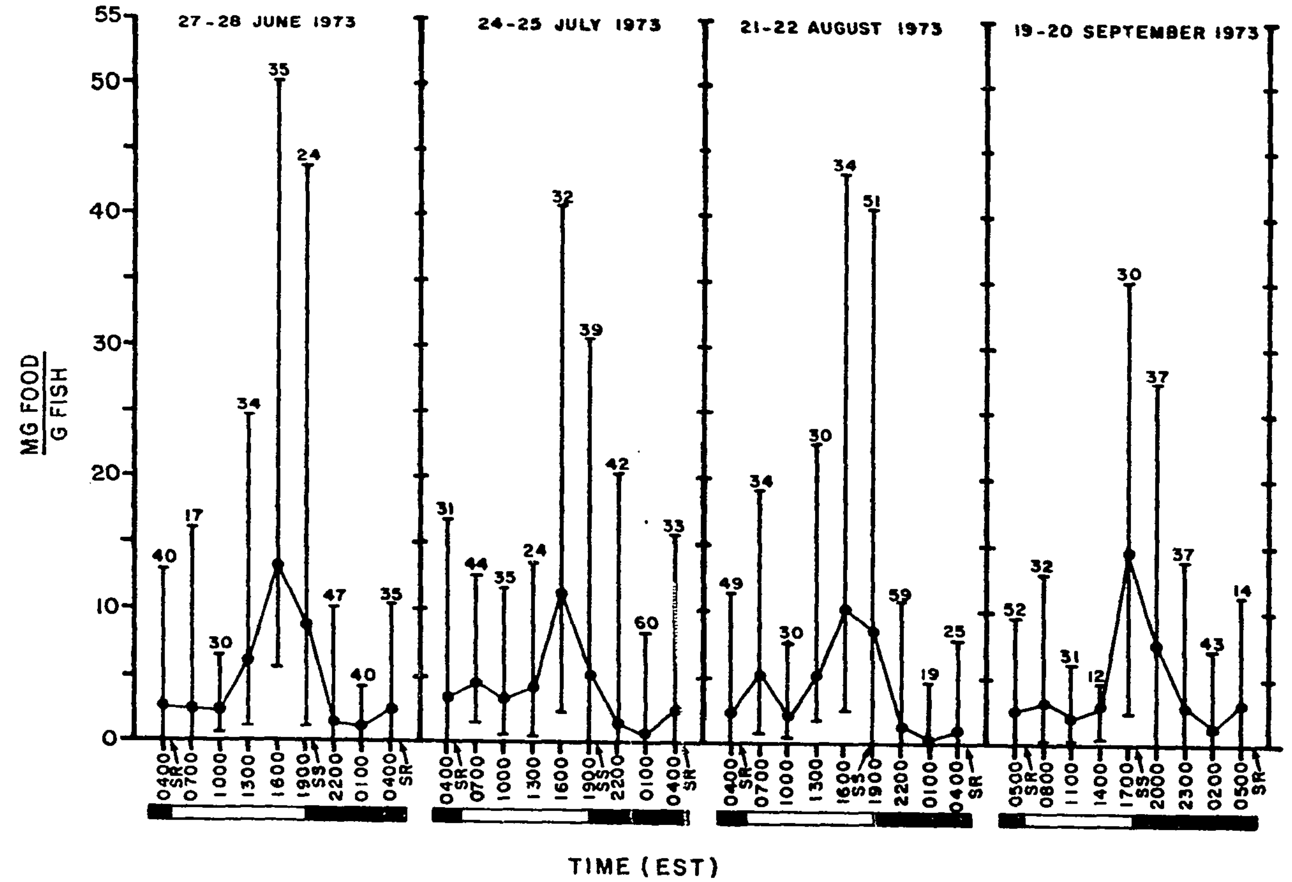

27-28 JUNE 1973
24-25 JULY 1973
21-22 AUGUST 1973
19-20 SEPTEMBER 1973
MG FOOD / G FISH
0
10
20
30
40
50
55
TIME (EST)
0400 SR 0700 1000 1300 1600 1900 SS 2200 0100 0400 SR
0400 SR 0700 1000 1300 1600 1900 SS 2200 0100 0400 SR
0400 SR 0700 1000 1300 1600 SS 1900 2200 0100 0400 SR
0500 SR 0800 1100 1400 1700 SS 2000 2300 0200 0500 SR
40 17 30 34 35 24 47 40 35
31 44 35 24 32 39 42 60 33
49 34 30 30 34 51 59 19 25
52 32 31 12 30 37 37 43 14

Figure 3. Total zooplankton standing crop at surface (vertical light bars) and midwater (vertical dark bars) at three hour intervals in monthly 27-hour stations during 1972 and 1973 in the James River, Virginia. (Horizontal bars below times indicate daylight and darkness)

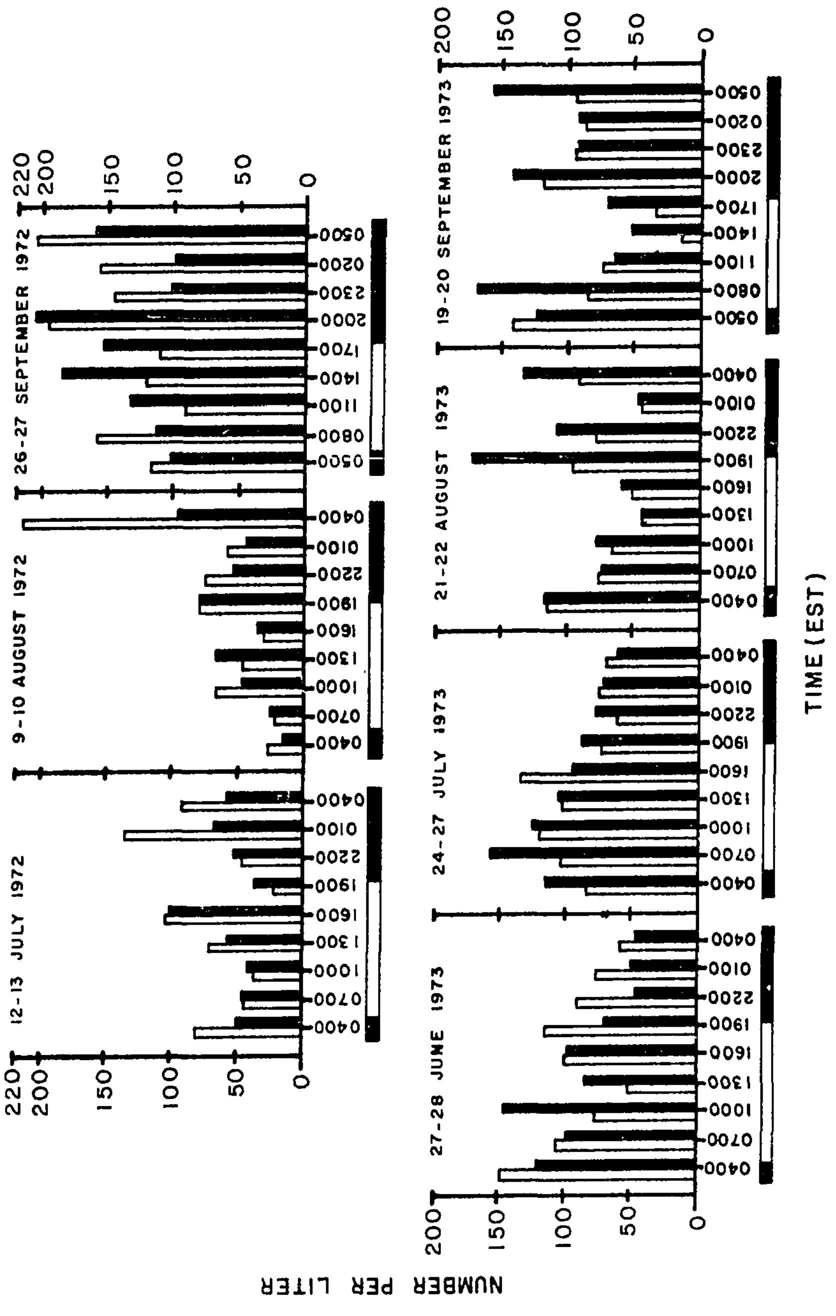

12-13 JULY 1972
9-10 AUGUST 1972
26-27 SEPTEMBER 1972
27-28 JUNE 1973
24-27 JULY 1973
21-22 AUGUST 1973
19-20 SEPTEMBER 1973
0
50
100
150
200
220
0400
0700
1000
1300
1600
1900
2200
0100
0500
0800
1100
1400
1700
2000
2300
0200
NUMBER PER LITER
TIME (EST)

Figure 4. Average day and night standing crop of predominant zooplankters at surface (light bars) and midwater (dark bars) in monthly 27-hour stations during 1972 in the James River, Virginia.

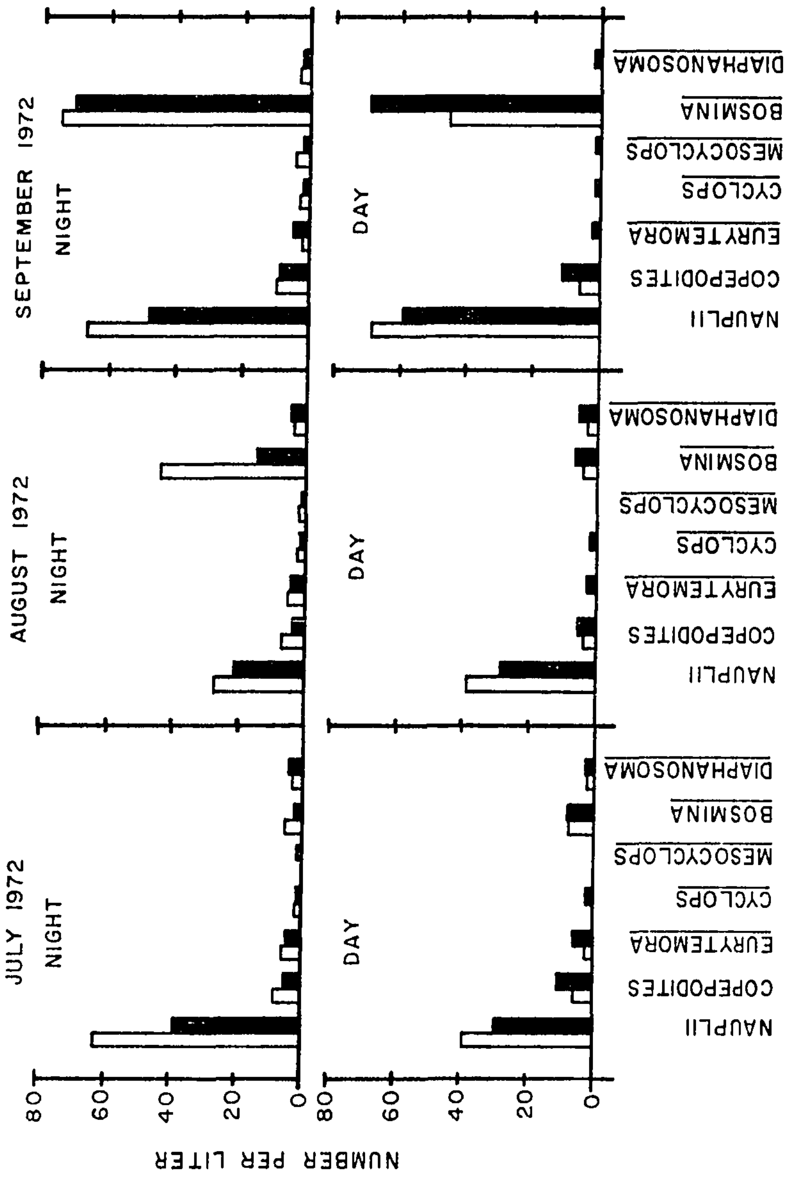

JULY 1972
AUGUST 1972
SEPTEMBER 1972
NIGHT
DAY
NUMBER PER LITER
0
20
40
60
80
NAUPLII
COPEPODITES
EURYTEMORA
CYCLOPS
MESOCYCLOPS
BOSMINA
DIAPHANOSOMA

Figure 5. Average day and night standing crop of predominant zooplankters at surface (light bars) and midwater (dark bars) in monthly 27-hour stations during 1973 in the James River, Virginia.

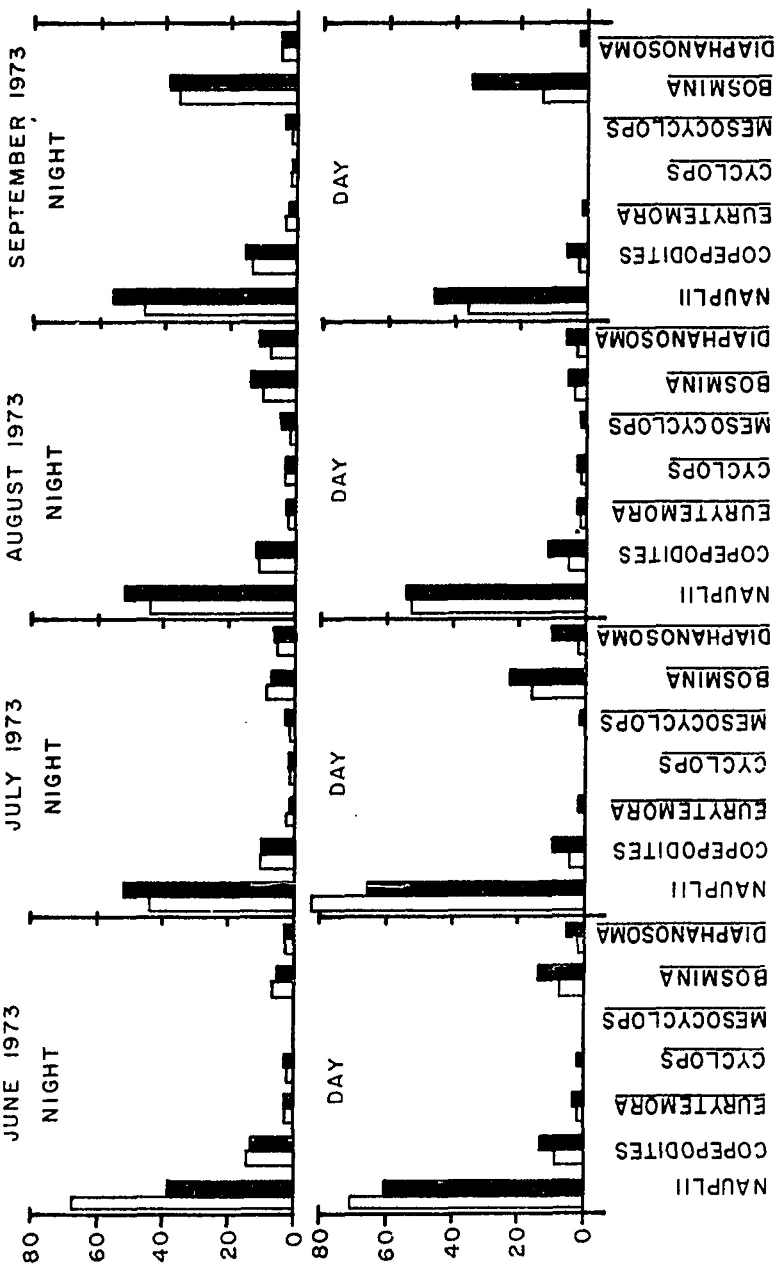
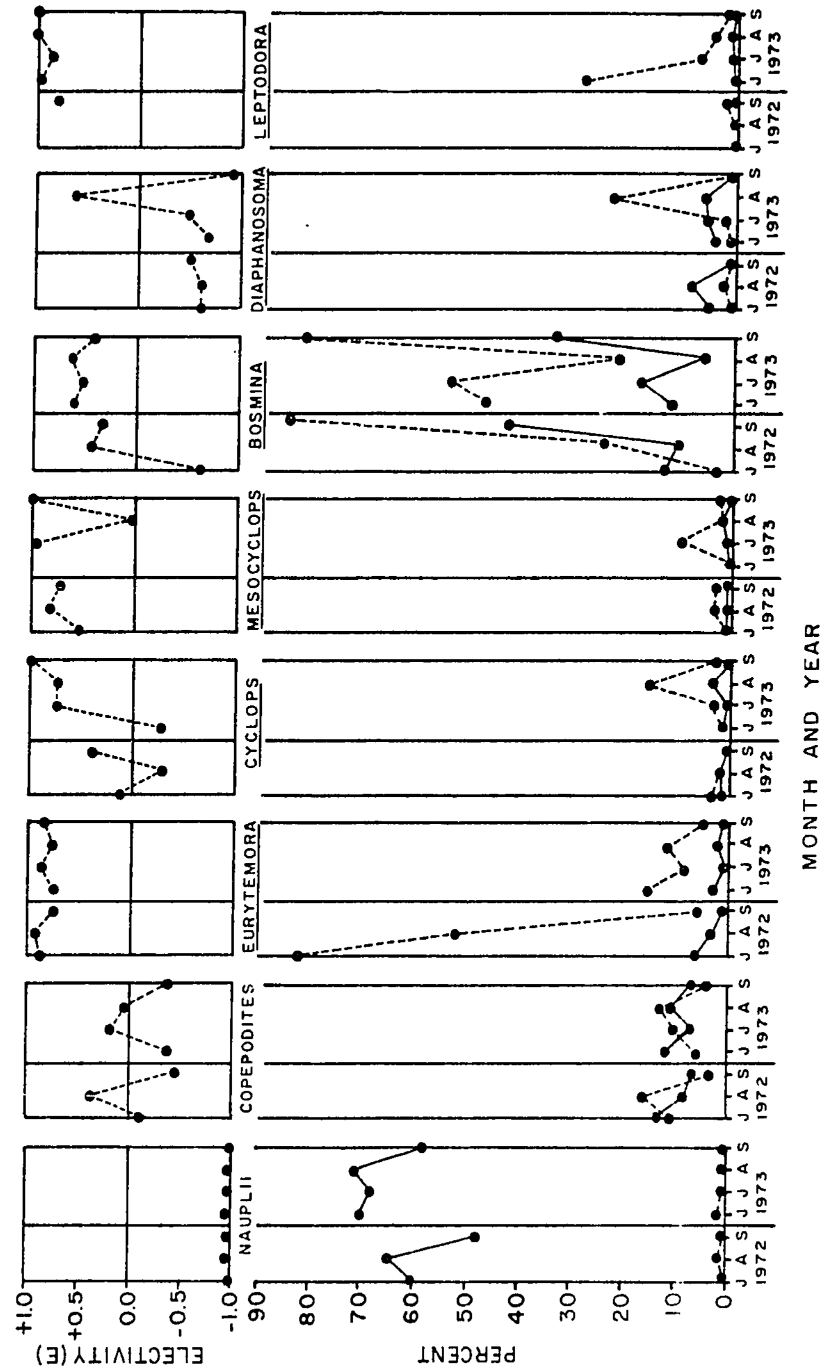

JUNE 1973
NIGHT
DAY
JULY 1973
NIGHT
DAY
AUGUST 1973
NIGHT
DAY
SEPTEMBER 1973
NIGHT
DAY
NAUPLII
COPEPODITES
EURYTEMORA
CYCLOPS
MESOCYCLOPS
BOSMINA
DIAPHANOSOMA
80
60
40
20
0
80
60
40
20
0

Figure 6. Average percent in the surface and midwater plankton (·——·——·) and stomachs (·----·----·), and electivity index (E), for selected zooplankters during the day from July through September 1972 and June through September 1973 in the James River, Virginia.


ELECTIVITY (E)
+1.0
+0.5
0.0
-0.5
-1.0
PERCENT
90
80
70
60
50
40
30
20
10
0
NAUPLII
COPEPODITES
EURYTEMORA
CYCLOPS
MESOCYCLOPS
BOSMINA
DIAPHANOSOMA
LEPTODORA
J A S J J A S
1972 1973
MONTH AND YEAR

CHAPTER II

ENERGY TRANSFORMATIONS BY JUVENILE ALEWIFE IN THE JAMES RIVER, VIRGINIA

ABSTRACT

Energy transformations by juvenile alewife, Alosa pseudoharengus, in the nursery area of the James River, Virginia, were estimated in 1972 and 1973 by laboratory and field methods. Preliminary estimations of daily rations were determined directly by ash-free caloric value of stomach contents in alewife collected every three hours during 27-hour stations, with laboratory-derived corrections applied for caloric value remaining from prior meals at mean environmental temperature. Percent egested of the caloric value of ingesta was estimated in the laboratory and ranged from 18% at 25 C to 29% at 30 C. Mean wet weight of all fish collected each month was converted to dry weight and caloric equivalent based on caloric analysis of ten fish each month, and the differences in caloric value between time intervals were calculated for estimation of growth rates. The caloric value of the remainder after growth was subtracted from assimilation was assigned to maintenance, since laboratory estimates of respiration rates were consistently high possibly due to handling of the excitable fish.

Ash-free caloric value of fish biocontent, daily ration, egesta, assimilation, and respiration increased from early summer through September in each year. Mean gross growth efficiency was 37% and 28% in 1972 and 1973 respectively and net growth efficiency was 48% and 37% in

1972 and 1973 respectively. Mean maintenance efficiency was 52% in 1972 and 63% in 1973. Lower water temperatures in 1972 may partially account for these differences, although flooding was prevalent in the early summer 1972.

INTRODUCTION

This report summarizes a two year investigation, based on laboratory and field studies, of energy transformations by juvenile alewife, Alosa pseudoharengus (Wilson), in the nursery area of the James River, Virginia.

Ecologists have historically concentrated on elucidating structure of populations. Through the impetus given by development of a model of trophic-dynamics (Lindeman, 1942), application of the energetics approach in animal sciences (Brody, 1945; Kleiber, 1961), and formulation of theoretical bioenergetic principles through synthesis of the literature (Winberg, 1956), modern research frequently attempts to define function in populations. Energy transformations in fishes are often investigated since fish production is of economic interest. Reviews on aspects of bioenergetics in fishes have appeared recently (Mann, 1967; Beamish and Dickie, 1967; Warren and Davis, 1967; Davis and Warren, 1971). Complete energy budgets have been developed for sand goby (Healy, 1972), perch (Soloman and Brafield, 1972), sargassum fish (Smith, 1973), ninespine stickleback (Cameron and Kostoris, 1973), blueback herring (Burbidge, 1974), and white bass (Wissing, 1974). Energy budgets of single species provide a common caloric basis for comparisons of different organisms in a variety of habitats and niches and are also useful in formulation of energy flow models for ecological systems.

MATERIALS AND METHODS

Laboratory Studies. Juvenile alewife were collected with a 30 m beach seine at Jamestown Beach (65 km from James River mouth) in September through November 1972 and 1973 for laboratory studies on respiration, stomach evacuation, and egestion rates. Since alewife are fragile fish, precautions and procedures for capture, handling, and transport developed for juvenile American shad were followed (Chittenden, 1971), except fungicide was added to the transport water to minimize infection due to injury. Fish were held in circular tanks in the laboratory at least six weeks before any experimentation to allow for initial mortality and adjustment to laboratory conditions. Fish were fed on *Artemia* nauplii twice daily during that period.

Respiration. Routine respiration rates under constant light at 20, 25, and 30 C were determined on eight fish at each temperature in a recording manometric respirometer (Wells and Warinner, 1968) submerged in a constant temperature bath (± 0.1 C). Fish were acclimated to experimental temperatures for at least 21 days and were fasted 48 hours before experimentation. Fish were allowed 12 hours to adjust to the 4.8 liter respirometer chamber before readings were recorded for a consecutive 24 to 60 hour period. A blank correction was run after removal of a fish and the apparatus subsequently cleaned. Fish were measured (68-80 mm fork length (FL), $\bar{X}$ = 73) and weighed (4.2-8.0 g wet weight, $\bar{X}$ = 5.7 g; 1.09-2.13 g dry weight, $\bar{X}$ = 1.51 g). Results were expressed in mg O_2 per gram fish weight per hour at standard temperature and pressure.

Stomach evacuation. Fish ranging from 55-81 mm FL and 2.5-8.1 g wet weight were acclimated at least 21 days to 20, 25, or 30 C (± 0.5 C) in three 110 liter aquaria under constant light. Fish were fed twice daily with *Artemia* nauplii until fasting began 48 hours before experimental feeding. A known wet weight of live mixed cladocerans and copepodite and adult cyclopoids, taken with a #10 (0.153 mm) mesh plankton net from a freshwater lake near White Marsh, Virginia, was introduced into each aquarium and fish were allowed to feed voluntarily for 30 minutes. About 45 mg of prey were potentially available to each fish (1.2% of mean fish wet weight). Six fish were sacrificed after 30 minutes from each aquarium and stomach contents weighed to the nearest 0.1 mg to establish average wet weight of ingesta for the single meal. Water filters were run to remove any uneaten prey. Six fish were sacrificed from each aquarium every 1.5 hours thereafter until wet weight of stomach contents averaged less than 1.0 mg. Dry weight, caloric value, and percent ash of stomach contents, pooled for each 1.5 hour interval at each temperature, were determined.

Egestion. Water filters were turned off at the termination of stomach evacuation experiments. Fecal matter produced over 48 hours by ten fish remaining in each aquarium at the specified water temperatures was collected with a pipette, pooled for each temperature, and frozen. This was later analyzed for dry weight, caloric value, and ash content. Feces of alewife were liberated as solid streamers and were easily seen. Feces were collected at 6-hour intervals to minimize bacterial contamination of the material. Fish were removed after 48 hours and water from each aquarium was siphoned through a # 20 (0.080 mm) mesh strainer to ascertain that no fecal matter was missed.

Field Studies. Data on daily feeding intensity and growth rates were taken during monthly 27-hour surface and midwater trawl stations in the James River near Hopewell, Virginia. Samples were taken at three hour intervals from July through September 1972 and June through September 1973 (Chapter I).

Feeding Intensity. Up to 25 alewife from the surface sample and 25 from the midwater sample during each three hour period were frozen on dry ice in the field. Stomach contents were carefully removed from thawed fish and wet weights determined individually to the nearest 0.1 mg. Dry weight, caloric value, and ash content were ascertained for the pooled surface and midwater sample each three hour period. In addition, data on wet weight of stomach contents of up to 5 alewife from the surface and 5 from midwater for each sample interval, (which were preserved in 10% formalin for prey identification, Chapter I), were combined with wet weight of contents from frozen fish to define feeding intensity as average wet weight stomach contents every three hours over 27 hours. Mean wet weight of stomach contents of both frozen and preserved fish was converted to mean dry weight by the mean percent weight of dry matter in the pooled stomach contents of frozen fish from each three hour period. Mean dry weight times mean ash-free (AF) caloric value per mg dry weight gave the total AF caloric value of stomach contents for each three hour period.

Growth. In addition to the fish preserved or frozen for feeding intensity analyses, all other alewife captured in both years were frozen on dry ice in the field. Thawed fish were measured to the nearest 1.0 mm FL and weighed to the nearest 0.1 g after removal of excess moisture. Ten randomly chosen fish from each of the seven sample months were dried in a 60 C oven for 36 hours and weighed to the nearest 1.0 mg after removal of stomach and intestine contents. Caloric value and ash content were determined for each of the ten dried fish per month. Wet weight of all alewife captured monthly was converted to dry weight by the mean percent weight of dry matter in the sample of dried fish. Monthly biocontent of all fish was calculated from the mean AF caloric content of the dried fish and mean dry weight data.

Bomb calorimetry. Sample material was dried in a 60 C oven for 24 hours, weighed to the nearest 0.1 mg, and stored if necessary in a dessicator. Grinding and mixing of samples were done in an automatic micromortar and pestle. Three bomb pills were prepared if sufficient quantity of a dried sample material was present. Each was weighed to 0.1 mg, and combusted in a Phillipson microbomb calorimeter (Phillipson, 1964) which was connected to a 0.0 - 1.0 mv recording potentiometer. Nitric acid and fuse wire corrections were applied to the resultant data. Ash content was determined from the dried remains of post-combustion pills, when quantities were limited, or from replicate combustions of additional sample material in a 600 C muffle oven for 12 hours. The calorimeter was standardized with three benzoic acid pills (6.314 cal/mg) before a daily series of determinations.

Energy transformations. Laboratory and field data were used to compute the daily terms of the balanced energy equation (Warren and Davis, 1967) for juvenile alewife:

$$C = F + U + R + \Delta B$$

Where: C = energy of ingesta (daily ration)

F = energy of egesta

U = energy of excreta

R = energy of respiration

ΔB = energy of growth

All energy calculations were based on the mean surface, midwater, and bottom temperature as determined at three hour intervals during monthly 27-hour stations.

Energy of ingesta between three hour sample periods over 27 hours was estimated as the total ash-free (AF) caloric value of stomach contents at a three hour sample period minus the percentage (Y) of that total caloric value remaining from prior three hour ($Y = 108.4000 - 2.3000 X$) and six hour ($Y = 53.1667 - 1.7200 X$) ingesta at the mean diurnal temperature (X). These corrections were based upon laboratory data for stomach evacuation of total caloric content at three and six hours for different temperatures. Caloric values of ingesta for each three hour sample period in the field were summed for 24 hours to give a preliminary estimate of daily ration.

Energy of egesta was estimated ($Y = -1.7167 + 0.9500 X$) as the percentage of the daily ration (Y) egested at mean diurnal temperature (X) on the basis of laboratory data for fish held at different temperatures. Energy of excreta was not estimated.

Energy of growth was derived from the change in mean AF caloric content of fish between monthly samples. After growth was subtracted from assimilation, energy of respiration was assumed to account for the remainder. Routine respiration rates for alewife were measured in the laboratory, but were not directly applicable to environmental conditions.

RESULTS AND DISCUSSION

Respiration. Routine respiration rates of juvenile alewife in the laboratory were relatively consistent and increased exponentially with increasing temperature (Fig.7). The rates were representative of single fish, which were fasted, briefly handled, and held under constant light. Mean rates ranged from 0.44 mg O_2/wet weight/hour at 20 C to 1.09 mg O_2 at 30 C and from 1.68 mg O_2/dry weight/hour at 20 C to 4.04 mg O_2 at 30 C. These rates were higher than those reported for other species of fishes (Winberg, 1956), although Burbidge (1974) cited similarly high rates for blueback herring (Alosa aestivalis).

Alewife swim constantly to maintain their position in the water column, and relatively high respiration rates are expected with such spontaneous activity. However, alewife are very prone to stress reactions; handling and confinement may have influenced the observed rates, although fish appeared calm after the initial adjustment period. The laboratory-derived rates were not used in energy transformation calculations. The remaining assimilated energy, after growth was estimated, was attributed to maintenance requirements in the energy budget, since alewife respiration in the environment integrates the responses to natural variability in temperature, dissolved oxygen, and photoperiodicity, feeding and escape reactions, and schooling behavior.

Stomach Evacuation. Mean wet weight of stomach contents decreased exponentially over time at each temperature based on a single meal, and dry weight decreased linearly (Fig.8). This suggests a rapid evacuation of fluids and a steady movement of solids. Although 45 mg wet weight of prey were potentially available to each fish, mean weight of stomach contents after 30 minutes (hour 0.0) was 32 mg at 20 C, 40 mg at 25 C, and 42 mg at 30 C. The times required for stomach evacuation decreased from 9 hours at 20 C to 6 hours at 30 C. These times were rapid compared to those cited for non-planktivorous fishes (Seaburg and Moyle, 1964; Windell, 1966; Tyler, 1970). Planktivorous juveniles of fishes, such as yellow perch (Noble, 1973) and white bass (Voightlander and Wissing, 1974), also exhibit rapid stomach evacuations at comparable temperatures.

Mean AF caloric values of stomach contents decreased linearly over time at each temperature (Fig.9). Mean values for single meal ingesta were 22 gram-calories (g-cal) AF at 20 C, 25 g-cal AF at 25 C, and 28 g-cal AF at 30 C. No values were calculated for 9 hours at 20 C or 7.5 hours at 30 C because of insufficient quantities of dried material for combustion. Linear regressions of experimental temperature (X) and percent of the AF caloric value of ingesta remaining (Y) after three hours ($Y = 108.4000 - 2.3000 X$; $r = -0.97$) and six hours ($Y = 53.1667 - 1.7200 X$; $r = -0.97$) were used as correction factors in the preliminary estimation of ingesta for fish captured at three hour intervals during 27-hour stations.

Factors other than temperature may affect digestion rates; size, condition, and behavior of fish, quantity and quality of food, and meal frequency are influential (Windell, 1967). Insufficient numbers of alewife were available for analysis of multiple meal effects on stomach evacuation. Alewife usually feed actively for several hours in the early morning and late afternoon (Chapter I), so multiple meals are most representative of natural feeding patterns. Multiple meals for gadoid fishes were evacuated 1.6 times as fast as single meals (Jones, 1974). Juvenile yellow perch (60 mm) at 15 C evacuated a single meal of zooplankters in 12 hours and a multiple meal in 6.1 hours; rates were even greater at 22 C when a single meal required 6.5 hours and a multiple meal 1.5 hours (Noble, 1973). Thus, stomach evacuation rates of alewife in the natural environment could be twice the rates observed in the laboratory for single meals.

Egestion. Total caloric content of egesta ranged from 4.3 g-cal AF at 20 C to 8.0 g-cal AF at 30 C (Table 3). A higher percent of the total AF caloric value of ingesta, from stomach evacuation experiments, was egested at 30 C (29%) than at lower temperatures. The lowest percent caloric egestion (18%) and the highest percent caloric assimilation (82%) occurred at 25 C; the percent egested (19%) and assimilated (81%) at 20 C was similar. These values approximate the range of assimilation efficiencies for other carnivorous fishes (Welch, 1968), although the value for assimilation at 30 C (71%) is rather low. Stomach evacuation in alewife at 30 C may be so rapid that mechanical and chemical breakdown of prey is very incomplete, yielding a reduced assimilation efficiency. However, assimilation in fishes such as red hind (Menzel, 1960) and walleye (Kelso, 1972) are independent of temperature.

A linear regression ($Y = -1.7167 + 0.9500$; $r = 0.82$) of experimental temperature (X) and percent egested (Y) of the caloric AF value of ingesta was used to estimate energy content of egesta in energy transformation calculations.

Ingestion. Energy of ingesta for alewife was calculated from field data as total AF caloric value of stomach contents each three hour interval during 27-hour stations, with laboratory-derived corrections for caloric value remaining from prior three and six hour ingesta. Calculations of ingesta for June 1973 (Table 4) give the method of computing preliminary daily ration, or the sum of ingesta over a consecutive 24 hours. The preliminary daily ration computed for that month (59 g-cal AF) was unusually low compared to other sample dates in 1972 (Table 5) and 1973 (Table 6).

The predicted caloric value of material remaining from prior meals often exceeded the total caloric value of stomach contents during periods of low feeding levels or non-feeding periods, which indicated that laboratory corrections for stomach evacuation rates based on single meals were too low. Thus, the preliminary daily ration values for each sample date were doubled in deriving the energy budget for juvenile alewife to account for the presumed effects of multiple meals, which would approximate the feeding pattern of alewife, on passage of food through the stomachs.

Estimation of the daily ration in fishes is difficult, and several general methods have been devised to conform to the requirements of particular studies (Davis and Warren, 1971). An advantage of the present method is the determination of caloric value of stomach contents directly, thus accounting for daily or seasonal changes in quantity or quality of prey. The method, however, is based on the assumption that laboratory evacuation rates are applicable to the field situation.

Growth. Mean fork length of alewife increased from 48 mm in July to 74 mm in September 1972 and from 46 mm in June to 65 mm in September 1973 (Fig.10). Mean wet weight increased from 1.5 g in July to 5.9 g in September 1972 and from 1.4 g in June to 4.4 g in September 1973.

Mean percent water in the wet weight of alewife decreased and percent ash in the dry weight as well as AF caloric value per g of fish increased from early summer through September in both years (Table 7). Fat deposits along the gastrointestinal tract of fish captured in September 1972 and 1973 were extensive, which may be important in the fall migration to the sea. Similar deposits were noted in juvenile white bass prior to overwintering (Wissing, 1974).

Growth in dry weight was rapid in 1972, ranging from 0.012 g/day for July - August to 0.020 g/day for August - September (Table 8). Growth rates in 1973 decreased from 0.015 g/day in June - July to 0.004 g/day in July - August and increased to 0.011 g/day in August - September. Growth rates in both years were greater than those reported for juvenile blueback herring in the James River during comparable time intervals in 1967 (Burbidge, 1974).

Energy Transformations. The AF caloric value for fish biocontent, ingestion, egestion, assimilation, and respiration for an alewife increased over the sample intervals in each year (Table 9). Growth rates in 1972, as g-cal AF/day, increased from 65 to 120 during the two time intervals. Growth rates in 1973, however, decreased from 86 in June - July to 24 in July - August and then increased to 63 in August - September.

Growth, as percent of assimilated energy (net growth efficiency), was highest (70.5%) June - July 1973 when respiration (maintenance efficiency) was unusually low (29.5%). Gross and net growth efficiencies were possibly overestimated and maintenance efficiency underestimated that sample interval due to the low daily ration calculated for the June sample date. Growth for other intervals in both years ranged from 15% to 55% of assimilated energy. These values are within the range reported for other fishes (Pandian, 1967 a,b; Brocksen et al.,1968; Smith, 1973; Wissing, 1974). Growth efficiencies are typically higher in younger fishes (Gerking, 1959). Maintenance efficiencies for alewife, excluding June - July 1973, ranged from 46% to 85%.

A greater mean portion of assimilated energy went into alewife growth in 1972 (48%) than in 1973 (37%), and, correspondingly, a lower portion was utilized in respiration in 1972 (52%) than in 1973 (63%). Mean water temperatures were cooler in 1972 than in 1973, although the months of June and July 1972 were characterized by several periods of high water due to Tropical Storm Agnes and other heavy rains.

Energy is an organizational factor in ecological systems. The ways that energy is partitioned in a community will affect the structure and function of a system. Knowledge of the feeding behavior and energy transformations of blueback herring (Burbidge, 1974) and alewife gives some insight into the dynamics of the fish community in the nursery area of the James River. Since juvenile alosine fishes compose up to 81% of the mainstream fish biomass during the late summer in the nursery grounds (Hoagman et al.,1973), interspecific competition is mainly among blueback, alewife, and American shad (Alosa sapidissima). There must be an effective niche or habitat segregation to mitigate competition for both food and space.

Both juvenile blueback herring and alewife feed selectively on the same species of prey in the zooplankton of the James River, which might indicate direct competition for food in the lighted surface waters. Juvenile American shad are also planktivorous (Hoagman et al., 1973). However, blueback herring typically feed continuously during the day with maximum stomach fullness occurring at sunset (Burbidge, 1974). Massmann (1963) reported greatest stomach fullness for American shad at dusk, and contents were observed to decrease during the night until most stomachs were empty at midday. Alewife usually exhibit a minor morning and a major afternoon feeding peak with maximum stomach fullness occurring about three hours before sunset in most months; some nocturnal feeding on immature and mature insects, ostracods, and oligochaetes also occurs (Chapter I). These differences in the timing of feeding could conceivably lessen the direct competition for food.

Blueback herring are more abundant in surface waters of the James River (Burbidge, 1974) and catch per unit of effort for alewife and American shad is usually greatest at midwater (Hoagman et al., 1973). Alewife and American shad possibly prefer a mid-depth habitat, with extended or intermittent movement to near surface waters primarily during peak feeding times. These differences in the micro-habitats of alosines in midstream could lessen competition for space. The abundance of these species and the degree of interspecific competition among the alosines in shoal waters or smaller tributaries are unknown and could alter the above considerations of food and space interactions.

Alewife typically attain a much larger size than blueback herring during the first summer of life in the nursery area of the James River (Hoagman et al., 1970). Growth, as percent of assimilated energy, ranged from 2.9% to 11.0% for blueback herring during the summer months of 1969, and maintenance efficiencies varied from 89.0% to 97.1% (Burbidge, 1974). The values for net growth efficiency for blueback herring are lower than those reported for alewife in the present study during comparable time intervals and similar water temperatures, and maintenance efficiency values were likewise higher for blueback herring than for alewife. The lower maintenenace requirements for alewife may partly explain the observed differences in production (growth) between the two alosine species in the nursery area.

The energy transformations of juvenile alewife in the James River were formulated from laboratory and field data, and their significance must be interpreted accordingly. As in any bioenergetics study, certain simplifying assumptions and estimations were necessary for the calculations. The results must be viewed as tentative since the validity of some assumptions, most notably that laboratory results are directly applicable to field situations (Kerr, 1971; Healey, 1972), is uncertain. Laboratory experimentation is the only method to attain certain results since some values, such as stomach evacuation, assimilation, and egestion rates, would be difficult to establish for alewife in the natural environment.

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Table 3. Dry weight and energy content (gram-calories ash-free) of ingesta and egesta from juvenile alewife, and percent of total ingested caloric value egested and assimilated at each temperature based on single meal experiments. (Numbers in parentheses are standard deviations for three replicate caloric determinations.)

	Ingesta			Egesta			Percent	
Water Temperature (C)	Mean Dry Weight (mg)	Mean Caloric Content (g-cal/ mg AF)	Total Caloric Content (g-cal AF)	Mean Dry Weight (mg)	Mean Caloric Content (g-cal/ mg AF)	Total Caloric Content (g-cal AF)	Egested	Assimilated
20	4.4	5.075 (0.060)	22.330	1.1	3.893 (0.187)	4.282	19.2	80.8
25	5.2	4.962 (0.028)	25.802	1.2	3.912 (0.183)	4.694	18.2	81.8
30	5.3	5.270 (0.061)	27.931	1.0	4.217 (0.150)	8.012	28.7	71.3

Table 4. Preliminary energy content (gram-calories ash-free) of ingesta from juvenile alewife collected at three hour intervals on 27-28 June 1973 in the James River, Virginia. (Preliminary daily ration = sum of ingesta for consecutive 24 hours; numbers in parentheses = standard deviations for replicate caloric determinations.)

	Stomach Contents					Corrections[a]		Ingesta
Time (EST)	Mean Wet Weight (mg)	Mean Dry Weight (mg)	Number of Bomb Pills	Mean Caloric Content (g-cal/ mg AF)	Total Caloric Content (g-cal AF)	Caloric Content Remaining Prior 3 Hour Ingesta (g-cal AF)	Caloric Content Remaining Prior 6 Hour Ingesta (g-cal AF)	Total Caloric Content (g-cal AF)
0400	3.1	0.9	2[c]	4.310 (0.072)	3.879	-	-	3.879
0700	3.3	0.9	1	4.632	4.169	1.761	-	2.408
1000	4.1	1.1	2	5.291 (0.056)	5.820	1.093	0.233	4.494
1300	6.6	2.1	3	5.558 (0.164)	11.672	2.040	0.144	9.488
1600	21.0	5.5	3	5.576 (0.106)	30.668	4.308	0.270	26.090

Table 4. (Continued)

	Stomach Contents					Corrections[a]		Ingesta
Time (EST)	Mean Wet Weight (mg)	Mean Dry Weight (mg)	Number of Bomb Pills	Mean Caloric Content (g-cal/ mg AF)	Total Caloric Content (g-cal AF)	Caloric Content Remaining Prior 3 Hour Ingesta (g-cal AF)	Caloric Content Remaining Prior 6 Hour Ingesta (g-cal AF)	Total Caloric Content (g-cal AF)
1900	13.6	3.8	3	5.620 (0.050)	21.356	11.845	0.569	8.942
2200	2.1	0.7	2	4.752 (0.081)	3.326	4.060	1.565	-2.299[b]
0100	2.1	0.6	2	4.515 (0.072)	2.709	0.000	0.000	2.709
0400	4.4	1.4	2	4.312 (0.046)	6.037	1.230	0.000	4.807
PRELIMINARY DAILY RATION (Σ 0700-0400 Ingesta)								58.938

Table 4. (Continued)

a. Mean water temperature = 27.4 C; 45.4% of total caloric value of stomach contents remains from prior 3 hour ingesta based on $Y = 108.4000 - 2.3000X$; 6.0% of total caloric value of stomach contents remains from prior 6 hour ingesta based on $Y = 53.1667 - 1.7200X$.

b. Negative ingesta considered as 0.000 in subsequent calculations.

c. When an insufficient quantity of dry matter was present to determine caloric value, as occurred occasionally in 1972 (Table 5), dry weight times an average of the mean caloric content of adjacent samples was used to estimate total caloric content.

Table 5. Preliminary energy content (gram-calories ash-free) of ingesta from juvenile alewife collected at three hour intervals in monthly 27-hour stations during 1972 in the James River, Virginia. (Preliminary daily ration = sum of ingesta for consecutive 24 hours.)

	Stomach Contents		Corrections		Ingesta
Date and Time (EST)	Number Stomachs Examined	Total Caloric Content (g-cal AF)	Caloric Content Remaining Prior 3 Hour Ingesta (g-cal AF)	Caloric Content Remaining Prior 6 Hour Ingesta (g-cal AF)	Total Caloric Content (g-cal AF)
12-13 Jul[a]					
0400	14	11.061	-	-	11.061
0700	23	19.928	6.039	-	13.889
1000	24	13.742	7.583	1.427	4.732
1300	60	27.724	2.584	1.792	23.348
1600	60	49.182	12.748	0.610	35.824
1900	41	41.119	19.560	3.012	18.547
2200	12	14.564	10.127	4.621	-0.184[e]
0100	8	3.984[d]	0.000	0.000	3.984
0400	0				
PRELIMINARY DAILY RATION (Σ0400-0100)					111.385
9-10 Aug[b]					
0400	20	8.648	-	-	8.648
0700	30	11.404	4.203	-	7.201
1000	3	4.873[d]	3.500	0.726	0.647

Table 5. (Continued)

	Stomach Contents		Corrections		Ingesta
Date and Time (EST)	Number Stomachs Examined	Total Caloric Content (g-cal AF)	Caloric Content Remaining Prior 3 Hour Ingesta (g-cal AF)	Caloric Content Remaining Prior 6 Hour Ingesta (g-cal AF)	Total Caloric Content (g-cal AF)
1300	13	38.445	0.314	0.605	37.526
1600	30	42.136	18.238	0.054	23.844
1900	21	32.410	11.588	3.152	17.670
2200	4	4.312^d	8.588	2.003	-6.279^e
0100	47	2.076	0.000	0.000	2.076
0400	17	1.417	1.009	0.000	0.408
PRELIMINARY DAILY RATION (Σ 0700-0400)					89.372
27-28 Sep^c					
0500	54	26.325	-	-	26.325
0800	31	39.427	13.768	-	25.659
1100	5	21.788^d	13.420	2.948	5.420
1400	29	51.625	2.835	2.874	45.916
1700	39	81.346	24.014	0.607	56.725
2000	37	70.472	29.667	5.143	35.662
2300	21	14.869	18.651	6.353	-10.135^e
0200	13	4.786	0.000	0.000	4.786
0500	21	22.291	2.503	0.000	19.788
PRELIMINARY DAILY RATION = (Σ 0800-0500)					193.956

Table 5. (Continued)

a. Mean water temperature = 23.4 C

b. Mean water temperature = 26.0 C

c. Mean water temperature = 24.4 C

d. See footnote c of Table 4.

e. Considered as 0.000 in subsequent calculations.

Table 6. Preliminary energy content (gram-calories ash-free) of ingesta from juvenile alewife collected at three hour intervals in monthly 27-hour stations during 1973 in the James River, Virginia. (Preliminary daily ration = sum of ingesta for consecutive 24 hours.)

	Stomach Contents		Corrections		Ingesta
Date and Time (EST)	Number Stomachs Examined	Total Caloric Content (g-cal AF)	Caloric Content Remaining Prior 3 Hour Ingesta (g-cal AF)	Caloric Content Remaining Prior 6 Hour Ingesta (g-cal AF)	Total Caloric Content (g-cal AF)
27-28 Jun[a]					
0400	40	3.879	-	-	3.879
0700	17	4.169	1.761	-	2.408
1000	30	5.820	1.093	0.233	4.494
1300	34	11.672	2.040	0.144	9.488
1600	35	30.668	4.308	0.270	26.090
1900	24	21.356	11.845	0.569	8.942
2200	47	3.326	4.060	1.565	-2.299[e]
0100	40	2.709	0.000	0.000	2.709
0400	35	6.037	1.230	0.000	4.807
PRELIMINARY DAILY RATION (Σ 0700-0400)					58.938
24-25 Jul[b]					
0400	31	14.067	-	-	14.067
0700	44	25.300	6.288	-	19.012
1000	35	13.998	8.498	0.774	4.726

Table 6. (Continued)

	Stomach Contents		Corrections		Ingesta
Date and Time (EST)	Number Stomachs Examined	Total Caloric Content (g-cal AF)	Caloric Content Remaining Prior 3 Hour Ingesta (g-cal AF)	Caloric Content Remaining Prior 6 Hour Ingesta (g-cal AF)	Total Caloric Content (g-cal AF)
1300	24	17.059	2.113	1.046	13.900
1600	32	54.924	6.213	0.260	48.451
1900	39	22.336	21.658	0.765	-0.087[e]
2200	42	6.980	0.000	0.000	6.980
0100	60	3.542	3.120	0.000	0.422
0400	35	10.302	0.189	0.384	9.729
PRELIMINARY DAILY RATION (Σ0700-0400)					103.220
21-22 Aug[c]					
0400	49	11.060	-	-	11.060
0700	34	27.199	5.121	-	22.078
1000	30	10.058	10.222	0.741	-0.905[e]
1300	30	24.040	0.000	0.000	24.040
1600	34	56.044	11.131	0.000	44.913
1900	51	40.869	20.795	1.611	18.463
2200	59	5.944	8.548	3.009	-5.613[e]
0100	19	2.623	0.000	0.000	2.623
0400	25	3.209	1.214	0.000	1.995
PRELIMINARY DAILY RATION (Σ0700-0400)					114.112

Table 6. (Continued)

	Stomach Contents		Corrections		Ingesta
Date and Time (EST)	Number Stomachs Examined	Total Caloric Content (g-cal AF)	Caloric Content Remaining Prior 3 Hour Ingesta (g-cal AF)	Caloric Content Remaining Prior 6 Hour Ingesta (g-cal AF)	Total Caloric Content (g-cal AF)
19-20 Sep[d]					
0500	52	17.969	-	-	17.969
0800	32	24.548	9.685	-	14.863
1100	31	12.102	8.011	2.228	1.863
1400	12	13.938	1.004	1.843	11.091
1700	30	130.597	5.978	0.231	124.388
2000	37	47.376	67.045	1.375	-21.044[e]
2300	37	16.875	0.000	0.000	16.875
0200	43	11.190	9.096	0.000	2.094
0500	14	18.929	1.129	2.093	15.707
PRELIMINARY DAILY RATION (Σ 0800-0500)					186.881

a. Mean water temperature = 27.4 C

b. Mean water temperature = 27.7 C

c. Mean water temperature = 27.0 C

d. Mean water temperature = 23.7 C

e. Considered as 0.000 in subsequent calculations.

Table 7. Length, weight, and caloric value of ten juvenile alewife collected each month from July through September 1972 and June through September 1973 in the James River, Virginia. (Numbers in parentheses = standard deviations of 30 replicate caloric determinations from sample of ten fish.)

Date	Mean Length (mm)	Mean Wet Weight (g)	Mean Dry Weight (g)	Mean Percent Water in Wet Weight	Mean Percent Ash in Dry Weight	Mean Caloric Content (g-cal/ g AF)
Jul 1972	50.9	1.6	0.380	76.2	10.0	5477 (208)
Aug 1972	57.2	2.6	0.685	73.7	10.1	5510 (135)
Sep 1972	75.9	6.1	1.691	72.3	11.2	5843 (113)
Jun 1973	45.2	1.3	0.313	75.9	9.8	5542 (127)
Jul 1973	57.3	3.1	0.797	74.3	10.2	5629 (187)
Aug 1973	60.1	3.6	0.932	74.1	10.3	5675 (168)
Sep 1973	64.7	4.5	1.198	73.4	10.7	5701 (122)

Table 8. Growth of juvenile alewife in the James River, Virginia for two time intervals during 1972 and three intervals during 1973.

Time Interval	Days	Mean Water Temperature (C)	Mean Length (mm)	Growth (mm/day)	Mean Dry Weight (g)	Growth (g/day)
12 Jul- 9 Aug 72	28	24.7	52.5	0.3	0.521	0.012
9 Aug- 26 Sep 72	48	25.2	65.8	0.4	1.159	0.020
27 Jun- 24 Jul 73	27	27.6	51.3	0.4	0.541	0.015
24 Jul- 21 Aug 73	28	27.4	58.1	0.1	0.800	0.004
21 Aug- 19 Sep 73	29	25.4	62.3	0.2	1.013	0.011

Table 9. Daily energy transformations by juvenile alewife in the James River, Virginia for two time intervals during 1972 and three intervals during 1973. (Gross growth efficiency = $\frac{\text{Growth}}{\text{Ingesta}} \times 100$; net growth efficiency = $\frac{\text{Growth}}{\text{Assimilation}} \times 100$; maintenance efficiency = $\frac{\text{Respiration}}{\text{Assimilation}} \times 100$.)

Caloric Content (g-cal AF)	Time Intervals						
	12 Jul- 9 Aug 72	9 Aug- 26 Sep 72	Mean 1972	27 Jun- 24 Jul 73	24 Jul- 21 Aug 73	21 Aug- 19 Sep 73	Mean 1973
Fish Biocontent	2862	6658		3031	4523	5761	
Ingesta	201	283		162	217	301	
Egesta	44	63		40	53	67	
Assimilation	157	220		122	164	234	
Respiration	92	100		36	140	171	
Growth	65	120		86	24	63	
Gross Growth Efficiency	32.3	42.4	37.4	53.1	11.1	20.9	28.4
Net Growth Efficiency	41.4	54.5	48.0	70.5	14.6	26.9	37.3
Maintenance Efficiency	58.6	45.5	52.0	29.5	85.4	73.1	62.7

Figure 7. Exponential regressions of oxygen consumption (0) as mg O_2/g wet weight fish/hour and mg O_2/g dry weight fish/hour for eight juvenile alewife at each temperature (T) and coefficients of determination (r^2). (Central horizontal line = mean; hollow bar = standard deviation; vertical line = range)

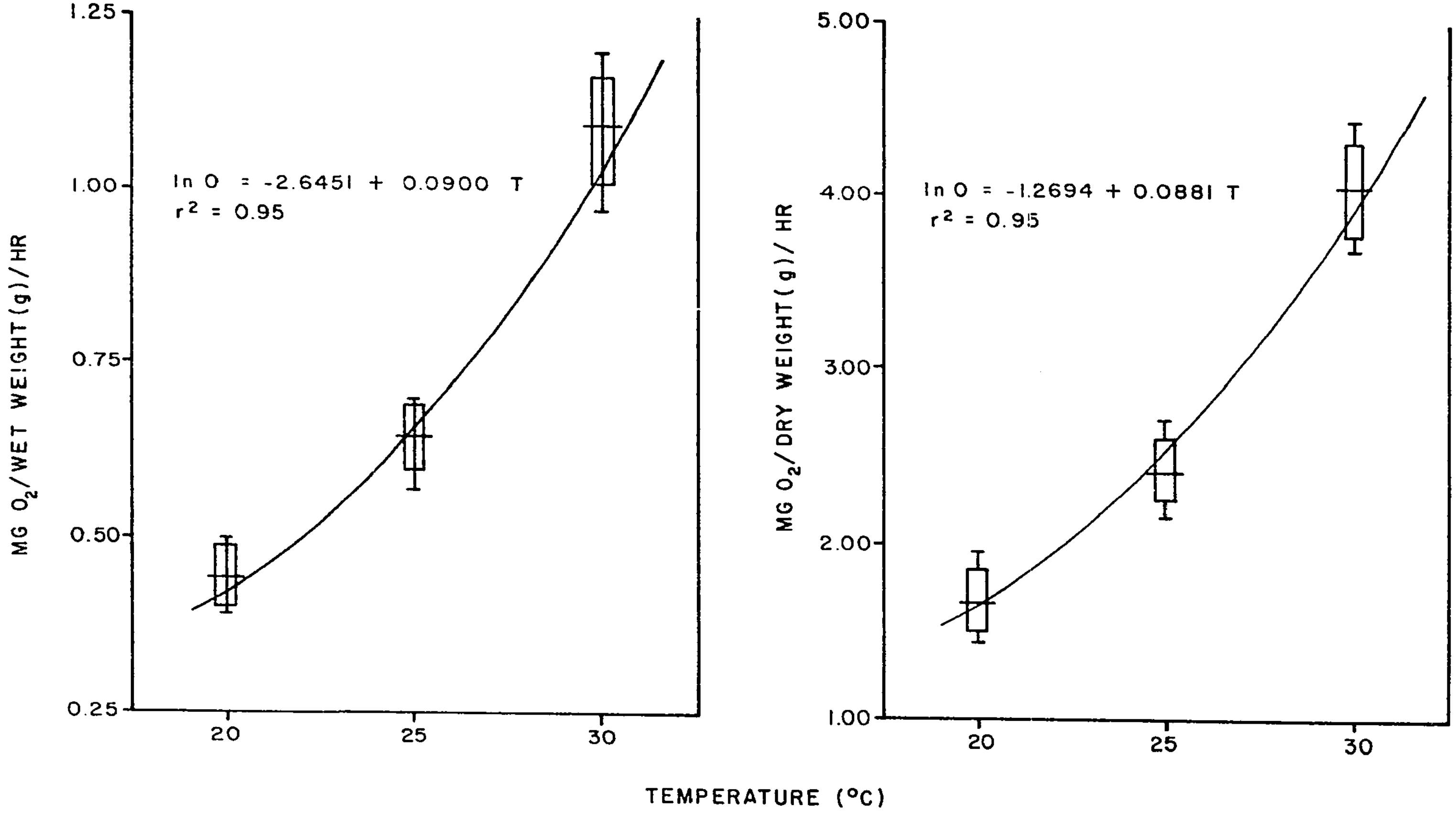

1.25
1.00
0.75
0.50
0.25
MG O_2/WET WEIGHT(g)/HR
ln O = -2.6451 + 0.0900 T
r^2 = 0.95
20
25
30
5.00
4.00
3.00
2.00
1.00
MG O_2/DRY WEIGHT(g)/HR
ln O = -1.2694 + 0.0881 T
r^2 = 0.95
20
25
30
TEMPERATURE (°C)

Figure 8. A. Exponential regressions of wet weight of stomach contents remaining (Y) at 1.5 hour intervals (X) after end of feeding at each temperature and coefficients of determination (r^2); B. Linear regressions of dry weight of stomach contents remaining (Y) at 1.5 hour intervals (X) after end of feeding at each temperature and correlation coefficients (r). (Central horizontal line = mean; hollow bar = standard deviation; vertical line = range)

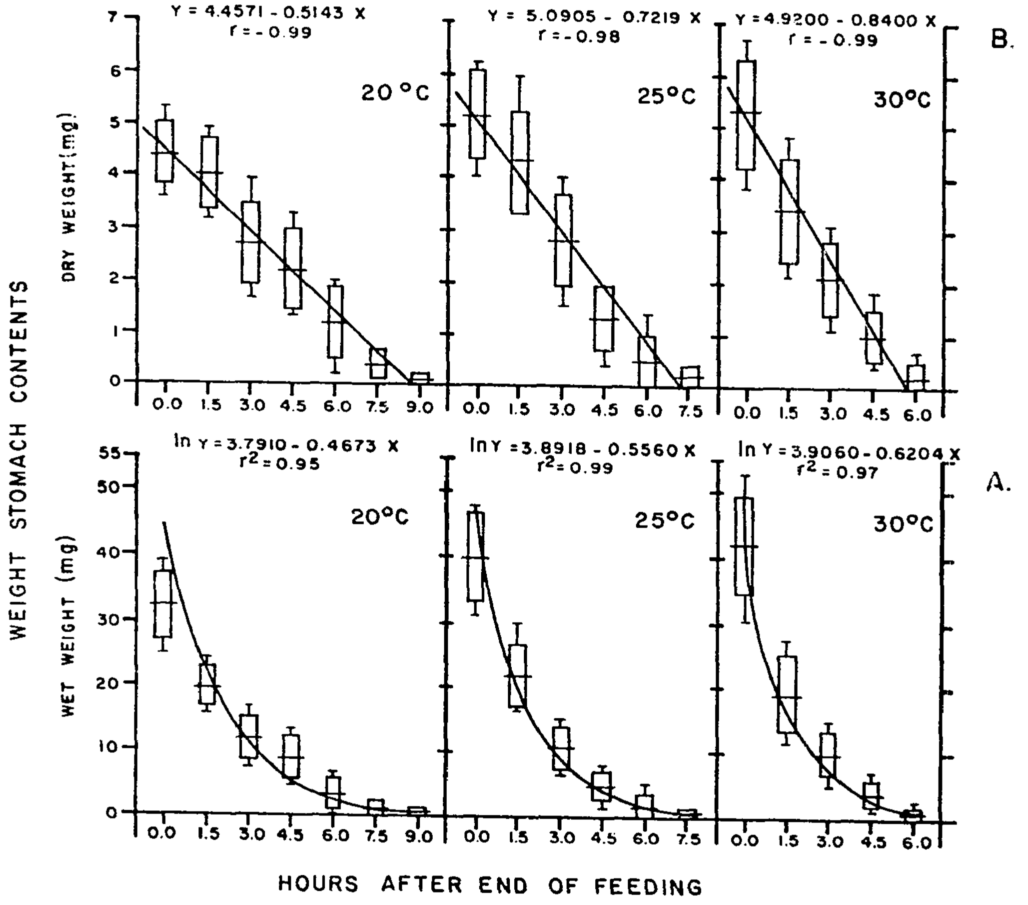

B.
A.
Y = 4.4571 - 0.5143 X
r = -0.99
20 °C
Y = 5.0905 - 0.7219 X
r = -0.98
25°C
Y = 4.9200 - 0.8400 X
r = -0.99
30°C
ln Y = 3.7910 - 0.4673 X
r2 = 0.95
20°C
ln Y = 3.8918 - 0.5560 X
r2 = 0.99
25°C
ln Y = 3.9060 - 0.6204 X
r2 = 0.97
30°C
WEIGHT STOMACH CONTENTS
DRY WEIGHT (mg)
WET WEIGHT (mg)
0
1
2
3
4
5
6
7
0
10
20
30
40
50
55
0.0 1.5 3.0 4.5 6.0 7.5 9.0
0.0 1.5 3.0 4.5 6.0 7.5
0.0 1.5 3.0 4.5 6.0
HOURS AFTER END OF FEEDING

Figure 9. Linear regressions of mean total caloric ash-free value of stomach contents remaining (Y) at 1.5 hour intervals (X) after end of feeding at each temperature and correlation coefficients (r).

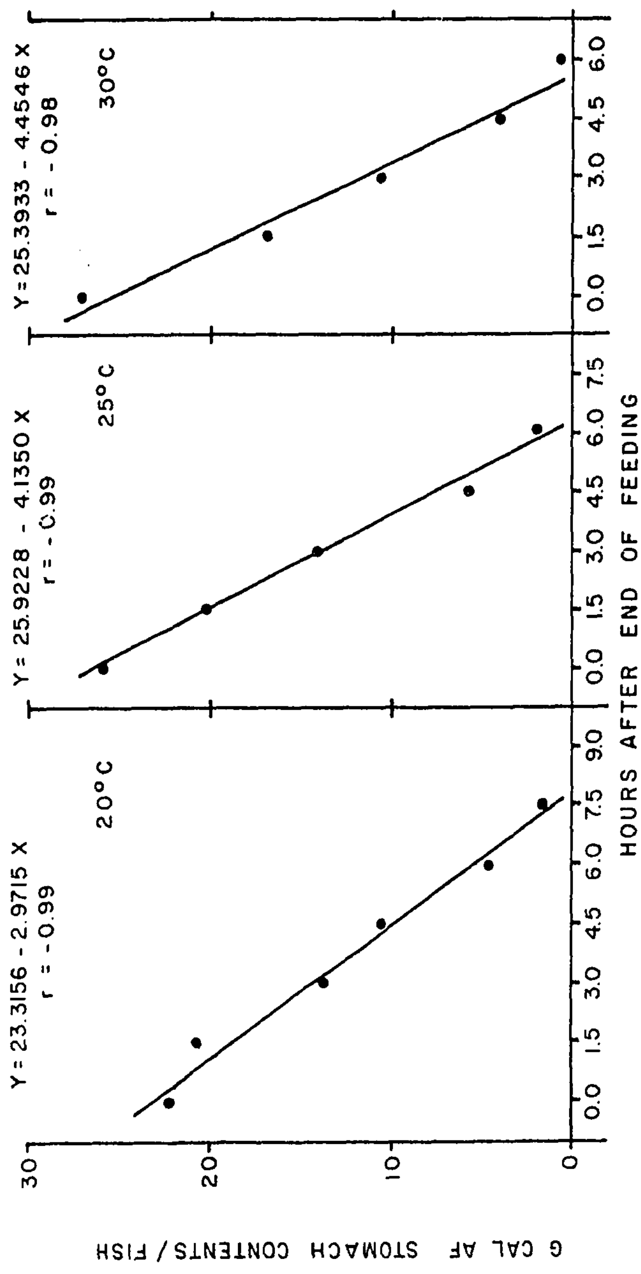
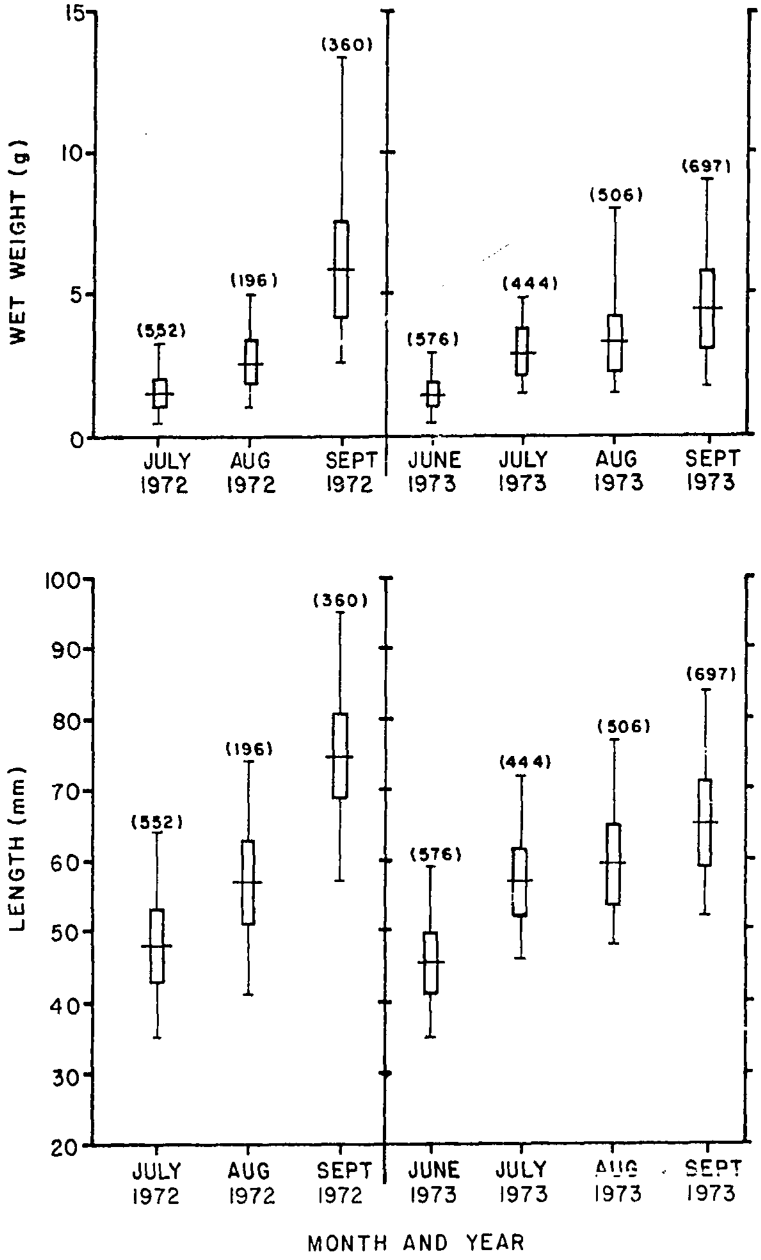

Y = 23.3156 - 2.9715 X
r = -0.99
20°C
Y = 25.9228 - 4.1350 X
r = -0.99
25°C
Y = 25.3933 - 4.4546 X
r = -0.98
30°C
0.0
1.5
3.0
4.5
6.0
7.5
9.0
HOURS AFTER END OF FEEDING
30
20
10
0
G CAL AF STOMACH CONTENTS / FISH

Figure 10. Length and wet weight of juvenile alewife captured in monthly 27-hour stations during 1972 and 1973 in the James River, Virginia. (Numbers in parentheses = total number of fish examined; central horizontal line = mean; hollow bar = standard deviation; vertical line = range)


WET WEIGHT (g)
15
10
5
0
(552)
(196)
(360)
(576)
(444)
(506)
(697)
JULY 1972
AUG 1972
SEPT 1972
JUNE 1973
JULY 1973
AUG 1973
SEPT 1973
LENGTH (mm)
100
90
80
70
60
50
40
30
20
(552)
(196)
(360)
(576)
(444)
(506)
(697)
JULY 1972
AUG 1972
SEPT 1972
JUNE 1973
JULY 1973
AUG 1973
SEPT 1973
MONTH AND YEAR

VITA

James Edwin Weaver

Born in Pensacola, Florida, 8 April 1946. Graduated Baker High School in Columbus, Georgia, June 1964. B.S. (Zoology), Louisiana State University, January 1968. M.S. (Fisheries), Louisiana State University, August 1969.

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